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ORIGINAL PAPER

Food choice of Antarctic soil arthropods clarified by stable isotope signatures

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Abstract Antarctic soil ecosystems are amongst the most simplified on Earth and include only few soil arthropod species, generally believed to be opportunistic omnivorous feeders. Using stable isotopic analyses, we investigated the food choice of two common and widely distributed Antarctic soil arthropod species using natural abundances of ^{13}C and ^{15}N and an isotope labelling study. In the laboratory we fed the isotomid springtail *Cryptopygus antarcticus* six potential food sources (one algal species, two lichens and three mosses). Our results showed a clear preference for algae and lichens rather than mosses. These results were corroborated by field data comparing stable isotope signatures from the most dominant cryptogams and soil arthropods (*C. antarcticus* and the oribatid mite *Alaskozetes antarcticus*). Thus, for the first time in an Antarctic study, we present clear evidence that these soil arthropods show selectivity in their choice of food and have a preference for algae and lichens above mosses.

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Introduction

Soil arthropods are known to play an important role in decomposition processes and nutrient flows through the soil ecosystem (Brussaard 1998; Filser 2002). However, detailed knowledge of the specific role of individual species in the soil ecosystem is necessary to better understand ecosystem processes (Faber 1991). Food availability is likely to be an important determinant of the functional composition of the soil arthropod fauna (Hodkinson and Wookey 1999), while their specific role in any soil ecosystem can only be understood in relation to their diet. The functional role of soil arthropods is generally very difficult to investigate, due to the complexity of most soil food webs. However, in the typically species-poor Antarctic terrestrial ecosystems the soil food web is relatively simple (Convey 2001), which makes them very suitable for addressing this type of question. However, to date very few studies have addressed this subject in Antarctic soil ecosystems, see review by Hogg et al. (2006).

Within Antarctic soils and vegetated ecosystems there are only a small number of arthropod species (Davis 1981; Usher and Booth 1986; Convey et al. 1996, 1997; Convey 2001; Sinclair 2001). However, the abundance of some of these arthropods (e.g. the isotomid springtail *Cryptopygus antarcticus*) can be very high, up to 10^6 individuals m^{-2} (Convey and Smith 1997), while communities are often dominated by only one or two species (Goddard 1979; Block 1982; Richard et al. 1994). These large numbers suggest that there

must be ample food available, and there is a generally accepted, but generally untested, assumption that food resources are not limiting for these arthropods (Convey 1996).

Maritime Antarctic vegetation is primarily composed of cryptogams (Longton 1967; Convey 2001) with mosses as the group that sequesters most of the carbon. As there are no large herbivores, almost all this carbon is transferred to the soil (Davis 1981). It has previously been suggested that most of the carbon and nutrients will flow directly into the decomposition pathway without passing through a consumer level (Block 1985). However, the contribution of the dominant groups of soil arthropods, springtails and mites, within these nutrient flows is not well understood.

Most existing data on feeding preferences of Antarctic soil arthropods is based on analysis of the gut content (Broady 1979; Burn 1981, 1984; Davidson and Broady 1996). This approach, while widely used, has the drawback that only the material that passes through the gut of an organism undamaged can be determined (Chamberlain et al. 2006a, b), while there is usually a large component of unidentifiable material remaining (Davis 1981). The use of stable isotopic analyses in soil food web studies has made it easier for ecologists to assess the role of soil organisms (Neilson et al. 1998; Briones et al. 1999; Scheu and Falca 2000; Schmidt et al. 2004; Staddon 2004). More importantly, assumptions about feeding preferences of species have been changed as a result of the use of this technique (Chamberlain et al. 2006a). Applying this technique on the components of Antarctic soil ecosystems will enable increased understanding of the feeding strategies of Antarctic soil arthropods, and of the specific roles these soil arthropods play in nutrient cycling in these ecosystems. Various studies have shown that the stable isotope signatures (δ^{13}C and δ^{15}N) of cryptogams differ considerably between species (Galimov 2000; Huiskes et al. 2006). These stable isotope differences in the producers should therefore lead to differences in consumer isotope ratios and assist in the determination of feeding preferences.

The aim of this study was to assess the food choice of the most dominant soil arthropods in maritime Antarctic soil ecosystems. We used two complementary approaches: (1) laboratory feeding-experiments with labelled and non-labelled food using *C. antarcticus* in order to determine which food sources are preferred by this species: and (2) a field survey on Anchorage Island (maritime Antarctic) in which we compared the isotopic signatures of the dominant springtail (*C. antarcticus*), mite (*Alaskozetes antarcticus*) and potential food sources.

Material and methods

Sampling site

Cryptogam and soil arthropod specimens were collected from Anchorage Island (maritime Antarctic). Anchorage Island is one of the Léonie Islands and lies in Marguerite Bay south of the Rothera Research Station of the British Antarctic Survey (67°61′S 68°22′W). The island is 2.5 km long and 500 m wide and is partly covered by semi-permanent snow and ice fields. The island includes several rocky ridges with a maximum height of 57 m a.s.l. On the slopes of these ridges, there are some patches of the moss *Sanionia uncinata* (Hedw.) Loeske, and the grass *Deschampsia antarctica* Desv. However, the vegetation consists mainly of lichens, with *Usnea antarctica* being most prominent.

Feeding experiments with the springtail *Cryptopygus antarcticus*

Cryptopygus antarcticus is by far the most abundant springtail in vegetated habitats of Anchorage Island (Convey and Smith 1997). Recent molecular phylogenetic research indicates that material currently referred to this species across its wide maritime and sub-Antarctic distribution is likely to represent several distinct lineages, with that from the Antarctic Peninsula referable to the subspecies *C. antartcticus antarcticus* (Stevens et al. 2006). Live specimens of *Cryptopygus* (henceforth referred to by generic name only) were transported to The Netherlands in plastic boxes with algae and mosses at 4°C. Two feeding experiments were performed. In the first experiment 20 individuals of *Cryptopygus* were placed in each of 30 polystyrene pots with a base of plaster of Paris. In all pots one of the following six food sources was placed: *Prasiola crispa* (alga), *Umbilicaria decussata* (lichen), *U. antarctica* (lichen), *S. uncinata* (moss), *Pohlia nutans* (moss) or *Brachythecium austrosalebrosum* (moss), each replicated five times. All these species occur naturally within local maritime Antarctic ecosystems. The pots were maintained in a climate chamber at 2°C for 6 weeks, the temperature being selected as it is the mean summer soil temperature at this location in the maritime Antarctic (S. Bokhorst et al. submitted). After this period, *Cryptopygus* and cryptogam samples were freeze-dried and analysed for their ^{13}C and ^{15}N content. *Cryptopygus* individuals were grouped together for each replicate in order to provide sufficient material for analyses (5 for ^{13}C and 15 for ^{15}N).

In the second experiment, the same six food sources were labelled with ^{13}C and ^{15}N. Labelling of the

cryptogams and alga with ^{13}C was achieved by placing moisturized parts of the above mentioned food sources in a desiccator with overhead lighting. Sodium bicarbonate (^{13}C, 99%, Cambridge Isotope Laboratories Inc., Andover, MA, USA) and hydrochloric acid were placed in the desiccator for 3 h to produce the labelled $^{13}CO_2$. The solution used for the ^{15}N labelling was based on a standard medium for culturing algae (Schlosser 1997). The original solution contained sodium nitrate, which we replaced with potassium nitrate (0.18 g labelled $K^{15}NO_3$ and 0.71 g non-labelled KNO_3) (^{15}N, 98%, Cambridge Isotope Laboratories Inc.). The solution was then sprayed onto the cryptogams once a day over a two-week period. *Cryptopygus* ($n = 20$ individuals) were then maintained with the labelled food sources for a period of 6 weeks, as described above ($n = 5$ pots for each food source). After the experiment two replicate pots from each food source were sampled and the cryptogams and *Cryptopygus* (individuals within each replicate were grouped together to obtain sufficient material) were freeze-dried and analysed for ^{13}C and ^{15}N.

Natural abundance of ^{13}C and ^{15}N in food items and soil arthropods

For this part of the study, we focussed on the dominant soil arthropods (the isotomid springtail *C. antarcticus* and oribatid mite *A. antarcticus*) that were readily collectable from the field. At Anchorage Island both species were collected from lichen, moss and alga-dominated communities. Arthropods were either shaken from pieces of the vegetation or removed with a small brush. Individuals ($n = 20$) were placed in glass containers and frozen to –20°C as soon as possible after collection (typically on the day of collection, on return to the research station). Cryptogams were sampled (1–2 g per sample, $n = 3$) from the location at which the arthropods were collected and also stored in glass container. All samples were stored at –20°C and transported to The Netherlands. The cryptogam samples ($n = 3$ per species) were freeze-dried and milled before analysis of ^{13}C and ^{15}N. Due to their small size, soil arthropods were freeze-dried but not milled prior to analysis. Individuals were grouped to provide sufficient material for analyses: *Cryptopygus*, $n \approx 5$ individuals, *Alaskozetes*, $n \approx 2$ individuals for each analysis.

Chemical analyses

Analyses of ^{15}N and ^{13}C were carried out using a Fisons NA 1500 elemental analyzer coupled to a Finnigan conflo II interface, and a Finnigan MAT Delta S isotope ratio mass spectrometer (IRMS). Due to the low concentrations of these isotopes, the isotopic ratios ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) were converted to delta units (δ) in parts per thousand, according to the formula:

$$\delta = \left(R_{sample}/R_{standard} - 1\right) \times 1,000$$

in which R is the molar ratio of heavy to light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). The standard ratio for carbon is V-PDB ($^{13}C/^{12}C \approx 1.124 \times 10^{-3}$) and for nitrogen it is atmospheric air ($^{15}N/^{14}N \approx 3.67 \times 10^{-3}$) (Dawson et al. 2002).

Statistical analysis

To control for non-homogeneity of variances, data were log-transformed prior to statistical analyses. Differences in stable isotope signatures between food types were analysed using a one-way ANOVA. A similar analysis was performed on the stable isotope signature of *Cryptopygus* obtained after feeding on different food types. In case of a significant main effect, differences among food items were a posteriori tested using Tukey HSD. Changes in stable isotope signatures of the food sources and of *Cryptopygus* as a result of labelling were tested with a factorial two-way ANOVA with species and labelling as independent factors. If there was a significant interaction between species and labelling the data were analysed for each species separately, using a one-way ANOVA. All analyses were completed using the program Statistica 7.0 (Statsoft Inc., Tulsa, OK, USA, http://www.statsoft.com).

Results

Feeding experiment

The variation in $\delta^{13}C$ values among the food items (±7‰) was considerably lower than the variation in $\delta^{15}N$ values (±25‰) (Fig. 1). Nevertheless, the food items differed significantly in $\delta^{13}C$ values ($F = 14.3$, $P < 0.01$). The three moss species had lower values than the two lichens, which were in turn lower than the alga, based on a Tukey HSD (Fig. 1a). The $\delta^{15}N$ of the food items also differed significantly ($F = 159.0$, $P < 0.001$). The lichens had the lowest values but there was considerable variation within this group. The mosses had higher values and were more closely grouped than the lichens. The alga had the highest value (17.0‰) based on Tukey HSD (Fig. 1b).

The $\delta^{13}C$ values of *Cryptopygus* did not differ after feeding on any of the available food sources after

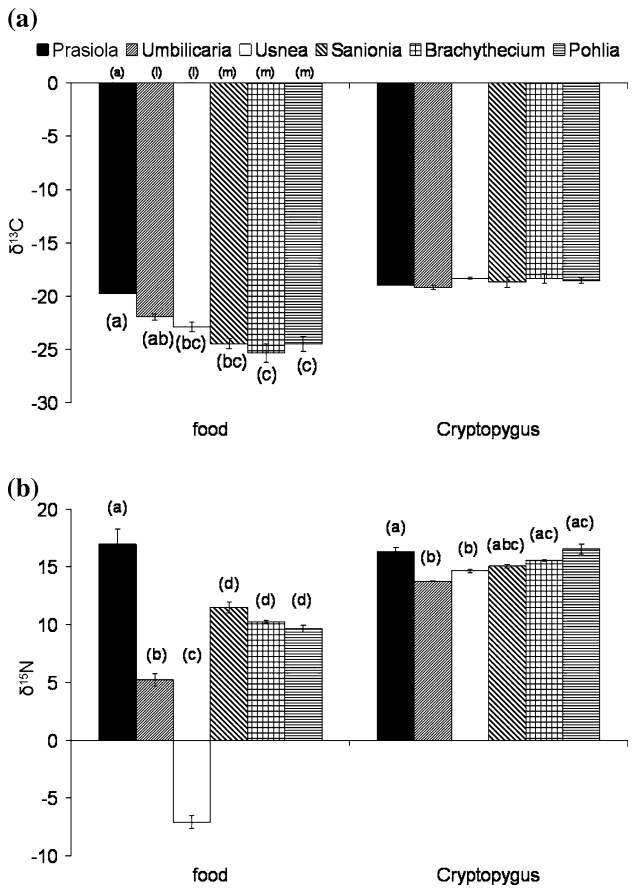

Fig. 1 Stable isotope contents (**a** δ^{13}C, **b** δ^{15}N) of food sources provided [mosses (*m*), lichens (*l*) and alga (*a*) indicated with the letters a, l and m between brackets], and of the springtail *Cryptopygus antarcticus* after having fed on the separate food sources for 6 weeks. Letters (a–c) between brackets indicate significant differences ($P < 0.05$) for food types and *Cryptopygus* separately, $n = 2$ for each *bar*, *error bars* indicated SE

6 weeks (Fig. 1a). However, the δ^{15}N values of animals fed on the two lichen species were slightly lower ($F = 12.2$, $P < 0.05$) than those provided with moss or algae. Given the lower δ^{15}N values of the lichens compared to the alga and the mosses (Fig. 1b) this suggests that these lower values are reflected in the isotopic signature of *Cryptopygus* when fed with lichens. Overall, the isotopic signatures of all the *Cryptopygus* examined were very similar to the stable isotope signature of the alga *P. crispa* (Fig. 1).

Experiment with labelled food

Labelling with ^{13}C had a significant effect on the ^{13}C signature ($F = 212.1$, $P < 0.001$) of the different food types presented. However, the increase in ^{13}C was not significant for all the moss species (Fig. 2a) as is reflected by the significant ($F = 60.8$, $P < 0.05$) interaction between species and labelling. Labelling of food increased ($F = 681.0$, $P < 0.001$) the δ^{15}N for all food types. The increase in ^{15}N was greater in the alga and lichens than the moss species (Fig. 2b), which was reflected by the significant ($F = 92.1$, $P < 0.001$) interaction between species and labelling.

For all food types, the δ^{15}N value of *Cryptopygus* increased ($F = 51.2$, $P < 0.01$) when provided with labelled food types. However when feeding on *Prasiola*, *Umbilicaria* and *Usnea*, the δ^{15}N increase was much greater than when feeding on the moss species (Fig. 3), indicating a preference for alga and lichens above moss. The δ^{13}C of *Cryptopygus* did not show a consistent change after eating labelled food.

The natural abundance of ^{13}C and ^{15}N of soil arthropods and cryptogams in the field

Moss and lichen species could be separated in two groups based on their δ^{15}N value (Fig. 4). Mosses had

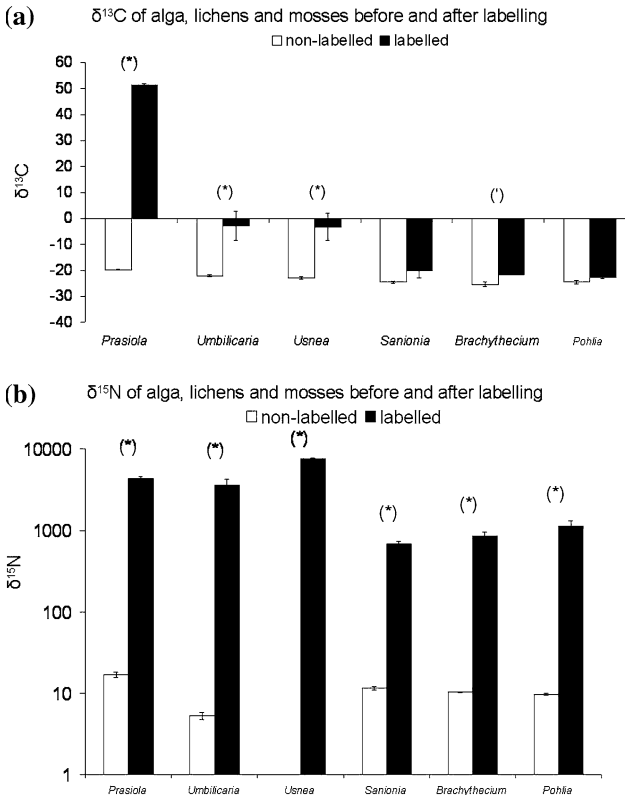

Fig. 2 Stable isotope contents (**a** δ^{13}C; **b** δ^{15}N) of the alga *Prasiola crispa*, the lichens *Umbilicaria decussata* and *Usnea antarctica* and the mosses *Brachythecium austrosalebrsoum*, *Sanionia uncinata* and *Pohlia nutans* from experiment 1 (non-labelled) and experiment 2 (labelled). Note the log scale on the y-axis of **b**. (*) and (') indicate significant and marginal ($P < 0.05$ and 0.1 Tukey HSD) differences between labelled and non-labelled δ values. $n = 2$ for each *bar*, *error bars* indicate SE

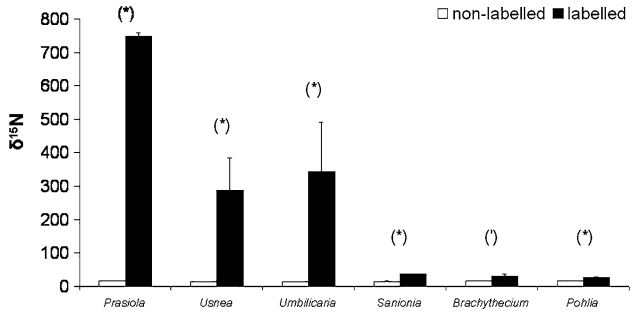

Fig. 3 Stable isotope (δ^{15}N) contents of *Cryptopygus antarcticus* after feeding for 6 weeks on δ^{15}N labelled (experiment 2) and non-labelled (experiment 1) food. (*) and (') indicate significant ($P < 0.05$ and 0.1 Tukey HSD) differences. $n = 2$ for each *bar*, *error bars* indicate SE

higher δ^{15}N values than lichen species, while the lichen species had large variability in their δ^{15}N value. The alga *Prasiola* had a similar δ^{15}N value to the moss species but the δ^{13}C value obtained from algae sampled amongst the lichen community was lower ($P < 0.01$) than in those samples obtained from the moss community (Fig. 4).

The δ^{13}C and δ^{15}N values obtained from field samples of *Cryptopygus* were similar to those of the alga *Prasiola*, indicating that this food type might be the main food source for this species. The other dominant soil arthropod *A. antarcticus* had higher δ^{15}N values than *Cryptopygus*. When sampled from a lichen community it had a lower ($P < 0.05$) δ^{13}C content than when sampled from the moss and alga community. As the alga *Prasiola* showed a similar separation in δ^{13}C it is highly likely that *Alaskozetes* also feeds primarily on alga. Overall these data indicate that algae are likely to be a dominant food resource for both these soil arthropod species.

Discussion

Food choice of antarctic soil arthropods

This study is the first to apply stable isotopic analyses to the study of the food webs of Antarctic soil ecosystems, although analogous studies have been successfully applied to Antarctic marine food webs (Kaehler et al. 2000; Gilpin et al. 2002; Jacob et al. 2006). This study had the primary aim of obtaining a better understanding of dietary selection in the most abundant isotomid springtail and oribatid mite of this region. When cultured on specific food types over a period of 6 weeks, the springtail *Cryptopygus* showed minimal changes in stable isotope signature except for a slight δ^{15}N decrease seen in those maintained on lichens. Analogous feeding experiments using temperate species maintained at higher temperatures have shown large changes in stable isotope composition of springtails after only 3–4 weeks (Briones et al. 1999). Therefore, the lack of response or very low response seen here could simply relate to the low temperature at which the experiment had to be maintained and/or the typically slow life cycle and development rates seen in Antarctic soil arthropods (Block and Convey 1995; Convey 1996).

Feeding with labelled food sources did result in a clear increase in δ^{15}N content when *Cryptopygus* was

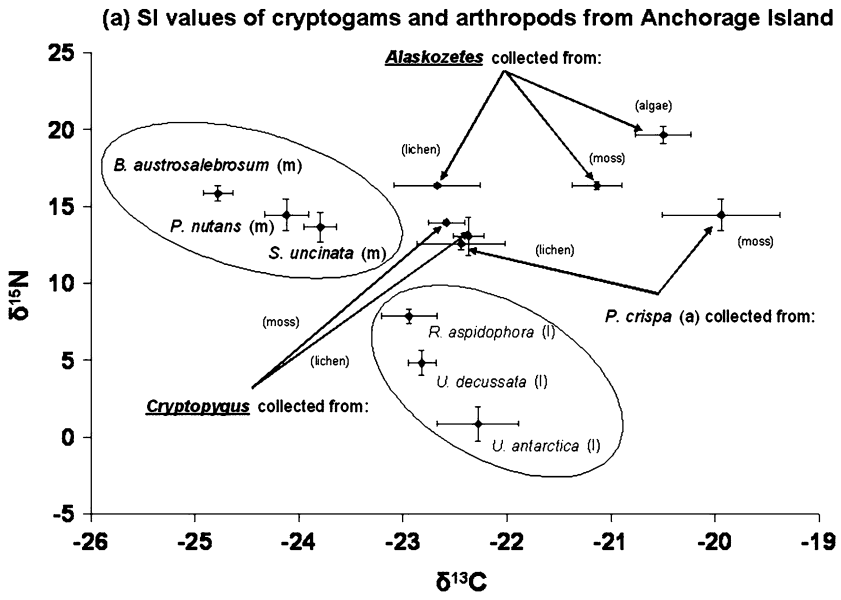

Fig. 4 Stable isotope (*SI*) (δ^{13}C and δ^{15}N) values of the dominant cryptogam species, *Prasiola crispa* (alga) and soil arthropods (*Cryptopygus antarcticus* and *Alaskozetes antarcticus*) from Anchorage Island. The circles group the lichen (*l*) and moss (*m*) species together based on SI values. The *arrows* indicate specific species collected from different community types. For all samples there was a minimum of three samples per species, *error bars* indicate SE

provided with the labelled alga and lichen species. The increase in δ^{15}N after feeding on moss was much lower. The ^{15}N labels of the food were not similar and may have affected the labelling of *Cryptopygus*. For instance, the ^{15}N content of the lichen *Usnea* was twice as high as that of *Prasiola*. The value found in *Cryptopygus* was, however, higher when feeding on *Prasiola* than on *Usnea*, indicating that more of the alga was consumed than of the lichen. The same principle applies to the feeding on moss. There was an increase of δ^{15}N in *Cryptopygus* from about 15 to 30‰ when feeding on moss, but they also had a δ^{15}N content of about 900‰ while a higher value would be expected if the moss was readily fed from. This indicates that moss is less attractive to this springtail as a food source. A possible reason for this is that mosses contain inhibitory or refractory compounds and are difficult for soil arthropods to digest (Lawrey 1987; Davidson and Broady 1996).

The natural abundance signatures obtained from the field survey are more difficult to interpret. Literature suggests that consumers generally increase in δ^{15}N content (±3 to 4‰) with every trophic level. For δ^{13}C the increase per trophic level is about 0.1–1‰ (Peterson and Fry 1987; Robinson 2001; Dawson et al. 2002). If a species feeds on food types that differ in stable isotope composition, it normally obtains a stable isotope signature intermediate between the sources.

The similarity in stable isotope signature between *Cryptopygus* and *Prasiola* suggests that *Cryptopygus* mainly feeds on this source but lacks the expected 3–4‰ increase in δ^{15}N content. However, if *Cryptopygus* simultaneously feeds on lichens that have a lower δ^{15}N signature, the mixing of these two sources could result in an intermediate value. That we do not find an intermediate value might indicate a higher preference for *Prasiola* above the lichens. Feeding by *Cryptopygus* during the second experiment also suggests a preference for *Prasiola* as *Cryptopygus* obtained the highest δ^{15}N signature when provided with the alga as compared to the other food types. This suggestion is further supported by the observation that this occurred even when the δ^{15}N value of the labelled lichen (*Usnea*) was almost twice as high as that of the alga (Fig. 2). *Cryptopygus* had higher δ^{13}C values than the three moss species, but the difference was relatively high (>1.0), which exceeds the expected value for a δ^{13}C increase from producer to consumer. Our feeding study thus suggests that *Cryptopygus* generally does not feed on mosses.

Although we have not attempted similar feeding experiments with *Alaskozetes* the results from the field study also suggest a preference for *Prasiola*. This is supported by the comparable difference in δ^{13}C values to the alga *Prasiola* when the latter was sampled from the lichen or the moss vegetation (Fig. 4). The δ^{13}C difference of *Prasiola* when sampled from lichen or moss vegetation might be attributed to water availability. Very wet conditions can slow down the diffusion of CO_2. This increases the internal CO_2 pressure and consequently the δ^{13}C content of the photosynthetic products increases, with less negative δ^{13}C values as a result (Lange et al. 1988). Similar results for *Prasiola* have been reported by Huiskes et al. (2006).

Compared to *Cryptopygus*, *Alaskozetes* had a high δ^{15}N signature (13‰ vs. 16‰). In the absence of autoecological knowledge, such an increase might be used to suggest that *Alaskozetes* would be a predatory species, or at least forms part of a higher trophic level (Schneider et al. 2004). However, existing literature gives no support to the proposal that *Alaskozetes* would be a predator species (Block 1985; Block and Convey 1995; Worland and Lukesova 2000). *Alaskozetes* can however, be abundant on and near animal carcasses (Goddard 1982), and feeding on such food sources and excreta may lead to a higher δ^{15}N signature. Care must therefore be taken when using stable isotope signatures in understanding food web interactions and trophic levels.

The role of soil arthropod in antarctic soil ecosystems revised?

Our study has focussed on two arthropod species from Anchorage Island. These two study species are numerically the most abundant representatives of their respective groups on this island (Convey et al. 1996). Combined with the fact that there are no larger herbivores in the Maritime Antarctic region (Convey 2001), their feeding preferences are the most likely of any arthropod to play an important role in nutrient cycling in the food web.

Previous studies based on analyses of gut contents have suggested that *Cryptopygus* feeds on algae, dead organic material, and fungi and thus is an unselective feeder (Tilbrook 1970; Broady 1979; Burn 1984; Block 1985; Cannon 1986). Our results in part support these earlier suggestions, with the caveat that only a limited range of potential sources within each class of food was included in our feeding experiments. Although moss fragments have been reported in the gut contents of springtails in some studies (Broady 1979; Davidson and Broady 1996; Varga et al. 2002), our findings show a more active preference for algae and lichens. Feeding preference by springtails in general is far from uniform (Walter 1987; Lee and Widden 1996; Maraun et al.

2003). Moreover, a study by Worland and Lukesova (2000) has shown that *Cryptopygus* shows selectivity even between different alga species. Based on our results and the existing literature this might suggest that *Cryptopygus* is a selective feeder.

In conclusion, our findings suggest that *Cryptopygus* plays a larger role in the nutrient flows from the algae- and lichen-dominated components of maritime Antarctic terrestrial food webs as compared to the moss-dominated element. *Alaskozetes* clearly showed some preference for alga but further study is required to clarify this species' role in nutrient flows. While clearly illustrating the potential of these techniques to be applied within Antarctic terrestrial ecosystems, more comprehensive studies of all the soil food web components and their autoecology is clearly necessary in order to understand the specific role played by each species in Antarctic soil ecosystems.

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